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Life Cycle Evolution in Asteroids: What is a Larva?

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Abstract. The diversity of larval forms and developmental patterns in asteroid echinoderms has become increasingly apparent over the past 10–15 years. However, the classification of developmental patterns has been ambiguous because the patterns have not been defined as unique sets of ecological and developmental character states. In addition, character states have not been defined consistently. Thus attempts to understand the evolutionary changes in development (*e.g.*, heterochrony and heterotopy in morphogenesis) that underlie larval diversity have been hampered. We propose a multifactor classification of asteroid developmental patterns that uses an explicit set of characters that provide information on habitat (*e.g.*, pelagic or benthic) and mode of nutrition (*e.g.*, feeding or nonfeeding) of the developing young, as well as the type of morphological development (indirect = larval; direct = nonlarval). We conclude that direct development is exceptionally rare. All asteroids whose development has been studied, except *Pteraster tesselatus*, have the indirect type of development. We also propose definitions of some important terms that have been used inconsistently in the literature (*e.g.*, larva, metamorphosis, indirect development, and direct development). Our definitions take into account the continuous nature of development and the evolutionary diversification of ontogenetic sequences. These definitions are intended to provide a clear conceptual basis for analyzing asteroid life cycle evolution. We argue that the ancestral asteroid life cycle involved pelagic larval development with both bipinnarian and brachiolarian stages. We then present a series of hypotheses for six types of evolutionary transitions in development that can account for the diversity of larval forms and developmental patterns in starfish.

Patterns of Development in Asteroids

Different schemes for classifying the patterns of development of marine benthic invertebrates have been applied to asteroids. In general, four different patterns (Table I) have been identified: (1) planktotrophy, (2) pelagic lecithotrophy, (3) demersal development, and (4) brooding (including viviparity) (Thorson, 1950; Mileikovsky, 1971, 1974; Chia, 1974; Jablonski and Lutz, 1983; Grahme and Branch, 1985). These patterns are distinguished largely on the basis of ecological characteristics, such as habitat or source of nutrition. The following descriptions of these major patterns of development outline the features that apply specifically to asteroids.

In the planktotrophic pattern, development involves a pelagic larva that feeds on suspended particles from the water column (*e.g.*, *Asterias rubens*, Gemmill, 1914; *Porania pulvillus*, Gemmill, 1915; *Astropecten aranciacus*, Hörstadius, 1939; *Astropecten scoparius*, Oguro *et al.*, 1976; *Patiriella regularis*, Byrne and Barker, 1991; see Emlet *et al.*, 1987, for an extensive list of asteroid species and patterns of development). Feeding larvae often have complex morphology and behavior associated with particle capture (Strathmann, 1974, 1987). A universal characteristic of species with planktotrophic development is the production of small eggs (≈100–250 μm) that contain insufficient nutritional reserves to support larval development to metamorphosis. Correlated with the very low levels of parental investment per offspring are extraordinarily high fecundities (ranging up to hundreds of millions of eggs per female per year). Because successful larval feeding is obligatory in species with the planktotrophic pattern of development, the duration of the larval period is often quite long (weeks to months), providing considerable potential for larval dispersal.

Pelagic lecithotrophy involves development via a pelagic nonfeeding larva (*e.g.*, *Solaster endeca*, Gemmill, 1912; *Crossaster papposus*, Gemmill, 1920; *Pteraster tesselatus*, Chia, 1966; McEdward, 1992; *Mediaster aequalis*, Birkeland *et al.*, 1971; *Astropecten gisselbrechti*, Komatsu and Nojima, 1985). Lecithotrophic larvae are morphologically simpler than related planktotrophic larvae, in that they lack feeding structures, such as ciliated bands

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Table I

Traditional classification of developmental patterns in asteroids with characteristics and examples

Name of pattern	Characters: Development[1]	Habitat	Nutrition[2]	Asteroid examples[3]
Planktotrophy	Indirect	Pelagic	Feeding	*Asterias rubens* *Astropecten scoparius*
Pelagic lecithotrophy	Indirect or direct	Pelagic	Nonfeeding	*Solaster endeca* *Astropecten gisselbrechti* *Pteraster tesselatus*
Demersal development	Indirect	Benthic	Nonfeeding or feeding	*Asterina minor* *Odontaster validus?*
Brooding	Indirect or direct	Benthic	Nonfeeding	*Leptasterias hexactis* *Pteraster militaris*

[1] Indirect and direct development are defined by the presence or absence, respectively, of a larval stage in development. These types of development are defined here using the restricted definition of a larva (see text).
[2] Feeding means that particulate nutrition is acquired from the seawater. Nonfeeding means that nutrition is acquired only from the mother.
[3] The examples provide a cross reference to those cited in the body of the paper.

or a mouth. In many cases, the only specialized structures that nonfeeding larvae possess are swimming structures or attachment organs for settlement to the benthos. Lecithotrophic larvae typically develop from much larger eggs than do planktotrophic larvae. As a consequence, species with lecithotrophic development have substantially lower fecundity relative to reproductive effort. These large eggs ($\approx$300–1500 μm) contain sufficient material to fuel development without larval feeding. In fact, most lecithotrophic larvae do not have a functional gut and are incapable of feeding. The pelagic period (days to weeks) provides the potential for at least some, and often considerable, dispersal from the parental site (Palmer and Strathmann, 1981).

Demersal development involves free-swimming larvae that remain very close to, or on, the benthos (*e.g., Asterina gibbosa,* MacBride, 1896; *Asterina minor,* Komatsu *et al.,* 1979; *Ophidiaster granifer,* Yamaguchi and Lucas, 1984; and perhaps *Odontaster validus,* Pearse and Bosch, 1986). Most species with demersal development have nonfeeding larvae that develop from relatively large eggs. Although the demersal period can be several months long (*e.g., Porania* sp., Bosch, 1989), the offspring are probably not dispersed great distances from the parental site. It is not yet known whether demersal larvae experience reduced predation risk compared with pelagic larvae.

Brooding involves the retention of the young by the parent on the benthos throughout development to the juvenile stage (*e.g., Leptasterias hexactis,* Chia, 1968; *Pteraster militaris,* Kaufman, 1968). Brooding is accomplished in a tremendous variety of ways, especially with respect to the degree of parental care and the location of the young. Offspring can be brooded internally in the stomach, in a specialized brood chamber (*e.g.,* under the supradorsal membrane of pterasterids), in the coelom, or in the gonad or externally under the oral surface or among the spines on the aboral surface. Several characteristics are common to all brooders. First, the lack of a pelagic phase in the life cycle greatly limits the potential for larval dispersal. Second, all brooded offspring rely exclusively on maternally provided nutrition. There is the potential for the transfer of nutritional materials from the parent to the offspring during the period of brooded development in some cases where the young are retained within the body of the parent (*e.g., Patiriella vivipera,* Chia, 1969; Byrne, 1991; *Pteraster militaris,* McClary and Mladenov, 1990; *Asterina pseudoexigua pacifica,* Komatsu *et al.,* 1990). Post-fertilization investment of resources by the parent complicates the picture, but in general, brooders produce eggs as large as, or larger than, related species with pelagic lecithotrophic development (Emlet *et al.,* 1987). Brooding is often correlated with small adult size and hermaphroditism (Strathmann and Strathmann, 1982).

The Problem

A developmental pattern is a complex entity that consists of a set of characters (*e.g.,* development, habitat, and nutrition) that describe the embryonic and larval stages of the life cycle. As discussed in the previous section, the character states of developmental patterns in asteroids are not perfectly correlated. For example, pelagic development can be associated with either feeding or nonfeeding development. Likewise, nonfeeding development can be associated with either indirect or direct development. Any effective classification of developmental patterns must be multifactorial in order to distinguish among the various possible combinations of the character states. There are eight patterns possible, based on three characters each with two states.

In the traditional classification, patterns are named and defined on the basis of the states of one (or at most two) characters. For example, demersal development is defined solely on the basis of habitat state (benthic). Consequently, there are two major problems: ambiguity and inconsistency. Ambiguity arises because only four patterns in the traditional classification attempt to encompass all of the possible combinations of the character states that describe a developmental pattern. Therefore the four traditional patterns do not distinguish unique sets of character states. Demersal development (Table 1) is an ambiguous definition of a developmental pattern because it does not distinguish between different nutritional (*i.e.*, feeding or nonfeeding) or developmental states (direct or indirect development).

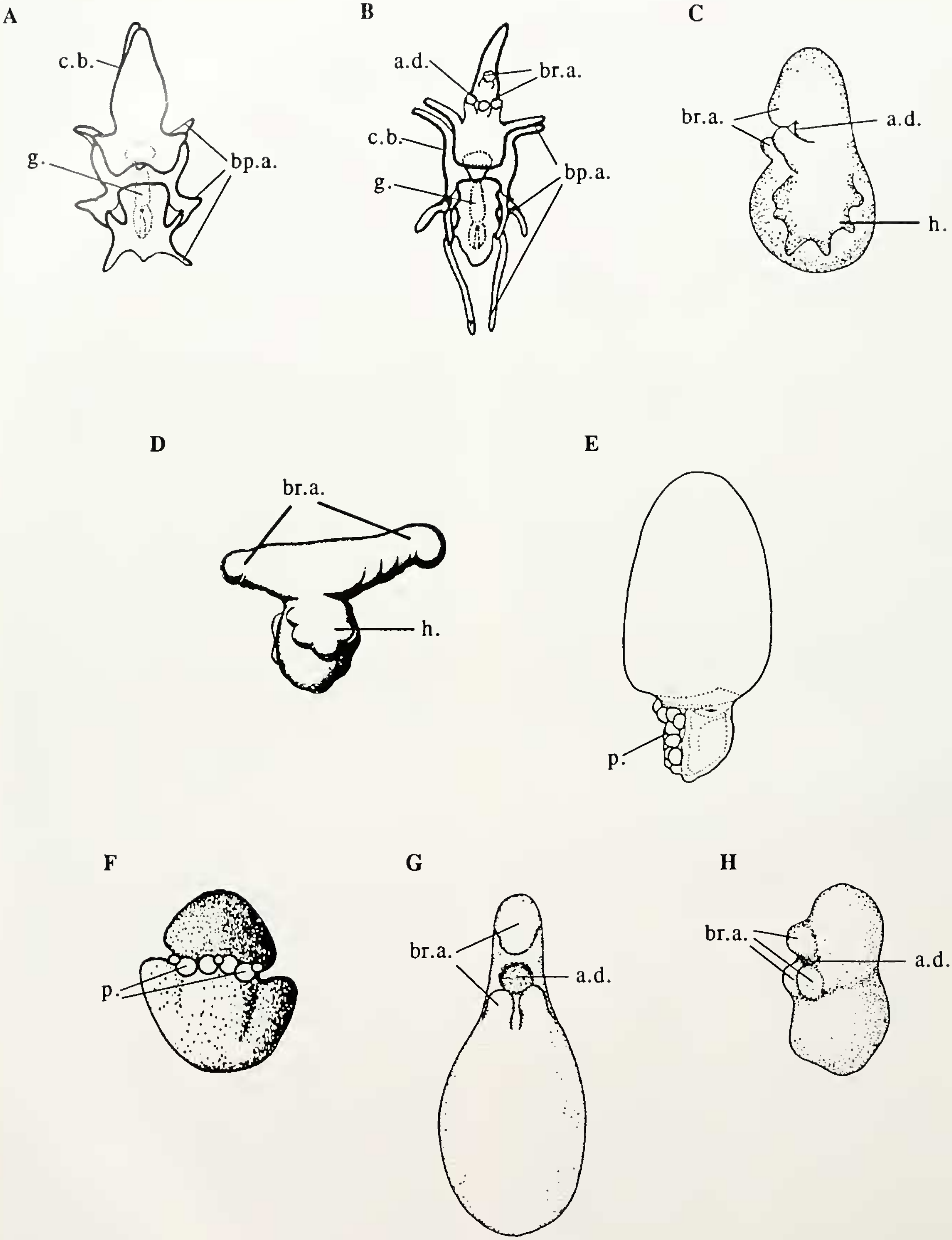
The traditional classification scheme is also inconsistent because some patterns, such as planktotrophy, are defined and named on the basis of one character (nutrition), whereas others, such as brooding, are defined on the basis of a different character (habitat). Inconsistency in the classification of developmental patterns also arises from the variable definition of character states (*e.g.*, direct or indirect development; see below) by different authors. The result of ambiguity and inconsistency is that the patterns of development described by the traditional classification cannot be mutually exclusive, and the classification must fail to adequately distinguish the existing patterns.

We think that there is an additional difficulty with the traditional classification. The definitions of developmental patterns emphasize ecological characteristics (habitat and nutrition) with little attention to the morphological nature of development (direct or indirect). As pointed out by Bonar (1978, p. 179), ecological descriptions of development have tended to mask the basic similarity of morphogenesis in many taxa. Conversely, they have also hampered the recognition of fundamental differences in morphogenesis (*e.g.*, *Pteraster tesselatus*, McEdward, 1992; Janies and McEdward, in review). To illustrate these points, we will survey the larval diversity and developmental characteristics in asteroid echinoderms. We will then propose explicit definitions of important terms and outline a multifactor classification scheme for developmental patterns.

Asteroid Larval Types

Starfish have two characteristic larval types: the bipinnaria and the brachiolaria (see Fell, 1967, p.S68). A bipinnarian larva (Fig. 1A) is characterized by the bilateral arrangement of the pre- and post-oral ciliated swimming and feeding bands that are borne on arms (MacBride, 1914, p.464; Kume and Dan, 1968, p.306). Bipinnarian arms are hollow extensions of the body wall; they contain blastocoelic space, but are not supported by calcareous skeletal rods. Although the number and size of bipinnarian arms varies among species, the arms can be identified by their anatomical location using the nomenclature designated by Mortensen (1898, pp: 6–7). The bipinnaria is a feeding larva and it occurs in the life cycle of all asteroids with planktotrophic larval development (*e.g.*, *Asterias forbesi*, *A. vulgaris*, Agassiz, 1877; *Luidia sarsi*, Wilson, 1978; *Patiriella regularis*, Byrne and Barker, 1991). A brachiolarian larva (Fig. 1B) is defined by the presence of specialized attachment structures on the preoral lobe: the brachiolar arms and attachment disk. Brachiolar arms are hollow, but contain extensions of the larval anterior coelom, and are thereby distinguished from bipinnarian arms (Gemmill, 1914; Barker, 1978). Brachiolar arms are used by larvae to test the substratum and provide initial, temporary adhesion during settlement. The adhesive disk secretes cement and provides more permanent attachment for metamorphosis. In asteroids with planktotrophic development, the brachiolarian stage only occurs after the bipinnaria (*e.g.*, *Asterias rubens*, Gemmill, 1914). Although these larvae are given different names, they are not independently evolved types of larvae, but rather sequential developmental stages.

Since the discovery of these asteroid larvae by Sars and Müller, several other larval types have been discovered. Some asteroids (*e.g.*, *Crossaster papposus*, Gemmill, 1920; *Echinaster echinophorus*, Atwood, 1973) develop via a nonfeeding pelagic brachiolarian larva (Fig. 1C). Nonfeeding brachiolarian larvae are morphologically simpler than planktotrophic brachiolarian larvae because they lack the ciliated band feeding structures, bipinnarian arms, and a functional gut. The most conspicuous larval structures that characterize both feeding and nonfeeding brachiolarian larvae are the attachment structures (brachiolar arms and attachment disk) and bilateral symmetry. Some asteroids develop via a benthic brachiolaria that has reduced brachiolar structures. For example, in *Asterina gibbosa*, the brachiolar arms are reduced to nonfunctional bulbs on a simple ciliated preoral lobe, but a functional adhesive disk remains (Fig. 1D) (Ludwig, 1882; MacBride, 1896). More typically, brooded brachiolaria retain well-developed and functional brachiolar arms and adhesive disks (*e.g.*, *Henricia sanguinolenta*, Masterman, 1902; *Leptasterias hexactis*, Osterud, 1918; Chia, 1968; *Henricia* sp., Chia and Walker, 1991; [= variety F, *H. leviuscula*, Fisher, 1911; p.282, according to Strathmann *et al.*, 1988]). Barrel-shaped larvae (Fig. 1E) occur in some species of paxillosids (*e.g.*, *Astropecten latespinosus*, Komatsu, 1975; Komatsu *et al.*, 1988, *Ctenopleura fisheri*, Komatsu, 1982; *Astropecten gisselbrechti*, Komatsu and Nojima, 1985). Barrel-shaped larvae are pelagic lecithotrophic larvae with abbreviated development and simplified morphology. *Pteraster tesselatus* has an unusual type of nonbrachiolarian pelagic lecithotrophic development (Chia, 1966; McEdward, 1992). A similar type of nonbrachio-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larian development also occurs in a brooder (Fig. 1F) (*Pteraster militaris*, Kaufman, 1968).

Appreciation of asteroid developmental diversity has increased over the past 10–15 years with the discovery of new larval types (*e.g.*, barrel-shaped larvae) and new developmental patterns [*e.g.*, demersal development, *Porania* sp., Bosch, 1989 (Fig. 1G); intragonadal ovoviviparity, *Asterina pseudoexigua pacifica*, Komatsu *et al.*, 1990 (Fig. 1H); and viviparity, *Pteraster militaris*, McClary and Mladenov, 1990]. This diversity has been described and classified largely according to the patterns outlined above (*e.g.*, planktotrophy, lecithotrophy, brooding, demersal development). The ambiguity and inconsistency inherent in the traditional classification scheme has hampered attempts to understand the evolutionary changes in development that underlie larval diversity. For example, the lack of correspondence between larval type and the traditional classification of developmental patterns in starfish is shown in Table II; the traditional classification scheme, cannot predict unambiguously the pattern of development, given the type of larva. Clearly the ecological and morphological characters of developmental patterns have evolved independently (*e.g.*, brachiolar attachment structures are often retained in brooded young).

Table II

Relationships between types of asteroid larvae and traditional patterns of development

Larval type	Developmental pattern
Bipinnaria	Planktotrophy
	Demersal development
Brachiolaria	Planktotrophy
	Pelagic lecithotrophy
	Demersal development
	Brooding
Paxillosid barrel-shaped larva	Pelagic lecithotrophy
Pterasterid nonbrachiolaria	Pelagic lecithotrophy
	Brooding
Developmental pattern	**Larval type**
Planktotrophy	Bipinnaria
	Brachiolaria
Pelagic Lecithotrophy	Brachiolaria
	Paxillosid barrel-shaped larva
	Pterasterid nonbrachiolaria
Demersal development	Bipinnaria
	Brachiolaria
Brooding	Brachiolaria
	Pterasterid nonbrachiolaria

Life Cycle Terminology

Many apparently simple terms are used to describe and interpret the diversity of development in asteroids. However, a consensus for the definition these terms does not exist. The problem stems in large part from the different contexts (*i.e.*, ecological or morphological) inherent in considerations of the evolution of marine invertebrate larvae. The discussion of terminology that follows is an attempt to provide a clear conceptual basis for analyzing evolutionary changes in asteroid life cycles. The application of these terms to specific developmental patterns and the resulting multifactor classification is discussed in the next sections.

Embryo

In general, embryos can be defined morphologically as cleavage stages, the blastula, and the gastrula. These are recognizable stages in the development of all animals, and in fact, the blastula and gastrula stages are defining features of the Metazoa (Buss, 1987; Bonner, 1988; Margulis, 1990). Hatching in asteroids occurs at various stages of development (blastula, gastrula, or later) and can therefore define neither the end of the embryonic period nor the beginning of the larval period. In the course of morphogenesis, structures specific to each group of organisms appear and gradually produce a definitive form (larval or juvenile). It is the seamless transition between the onset of morphogenesis and the achievement of a definitive form that makes the distinction between late embryo and early larva, or early juvenile, impossible to identify with precision. For this reason, the term "embryo" is best restricted to the stages of development that are of universal occurrence (cleavage, blastula, and gastrula) and should not be used to refer to the subsequent transitional period.

Larva

In spite of numerous attempts, no one has provided a precise and generally accepted definition of the term

Figure 1. Diagrams of various asteroid larval types. A. Complex feeding, pelagic bipinnaria (unidentified luidiid, *e.g.*, *Luidia foliolata;* modified from Strathmann, 1974, p.324); B. Complex feeding, pelagic brachiolaria (unidentified asteriid, *e.g.*, *Pisaster ochraceus;* modified from Strathmann, 1974, p.324); C. Simple nonfeeding, pelagic brachiolaria (*Solaster endeca*, modified from Hyman, 1955, p.298); D. Simple nonfeeding, benthic brachiolaria (*Asterina gibbosa*, modified from MacBride, 1896, pl. 18); E. Nonfeeding, pelagic barrel-shaped larva (*Ctenopleura fisheri*, modified from Komatsu, 1982, p.202); F. Simple nonfeeding, benthic nonbrachiolarian stage (*Pteraster militaris*, modified from Kaufman, 1968, p.508). G. Simple nonfeeding, benthic brachiolaria (*Porania* sp., modified from Bosch, 1989, p.80); H. Simple nonfeeding, benthic brachiolaria (*Asterina pseudoexigua pacifica*, modified from Komatsu *et al.*, 1990, p.259). Abbreviations: a.d., adhesive disk; bp.a., bipinnarian arm; br.a., brachiolar arm; c.b., ciliated band; g., gut; h., hydrocoel; p., podia.

"larva." We believe that such a definition is impossible for two reasons: (1) the continuous nature of development, and (2) the evolutionary diversification of development. First, "larva" refers to a stage (or series of stages) in a developmental sequence. In asteroids, development does not progress as a sequence of discrete instars but rather involves continuous changes in morphology. Stages cannot be precisely defined, because they do not begin and end with unambiguously identifiable developmental events. The larval form is produced by morphogenetic processes that gradually transform the embryo into a more complex shape. Larval stages transform into juvenile stages during metamorphosis, which can be rapid and drastic or prolonged and gradual. Second, developmental sequences may have been greatly modified (accelerated, retarded, and condensed), and the stages within those sequences may have undergone evolutionary modification. Given the tremendous morphological, ecological, and taxonomic diversity of marine invertebrates, it is not surprising that a single definition fails to be universally applicable.

For evolutionary studies, we maintain that a larva should be defined as an intermediate stage in the life cycle that is produced by post-embryonic morphogenesis and is eliminated by the metamorphic transition to the juvenile; in addition, this intermediate stage must possess transitory structural features that are not developmentally necessary for morphogenesis of the juvenile. Transitory larval features may be specialized for independent existence during development, or be reduced in derived modes of development.

Juvenile

The term "juvenile" has been used in a very broad sense. At one extreme, it refers to the "post-larval" stages, either immediately following abrupt metamorphosis from a definitive larval stage, or at some ill-defined point during a prolonged, gradual metamorphosis. At the other extreme, juveniles are "pre-adults" that have the definitive adult morphology, but are small or at least not sexually mature. For the present discussion, it is more important to establish criteria for defining the earliest juvenile stage. We suggest that a juvenile has attained the adult body plan (symmetry, general body shape), and the major systems are functional (especially locomotion and feeding, but not reproduction). This definition intentionally excludes the transitional period during metamorphosis.

Metamorphosis

This literally means a change in morphology. But as was stated above, the entire developmental process produces continuous changes in form. "Metamorphosis" has often been restricted to cases where there is a drastic and rapid change in morphology. However, it is more useful to consider metamorphosis as the transition from the larval body plan to the juvenile body plan, regardless of the rate or magnitude of the change. Metamorphosis then requires a definitive larval stage in the life cycle, and its occurrence thus defines the indirect pattern of development.

Indirect development

This refers to a pattern of development in which the embryo is followed by intermediate stages with structural features that are not directly involved in the morphogenesis of the juvenile (Fig. 2). These intermediate stages are larvae and by virtue of having a specialized structure and a transitory body plan must undergo a metamorphosis to the juvenile body plan. The construction of larval morphology (*e.g.*, specific organs or overall body symmetry) defines the indirect nature of a developmental sequence. Larval structures might, but need not be functional during development. A brooded larva that does not swim in the water column or settle to the benthos may still possess the structures for swimming and settlement.

Direct development

This refers to a pattern of development wherein the embryonic stages are followed by the morphogenesis of the juvenile, without an intervening larval stage. The idealized life cycles in Figure 2 illustrate the importance of the larval stage in distinguishing between direct and

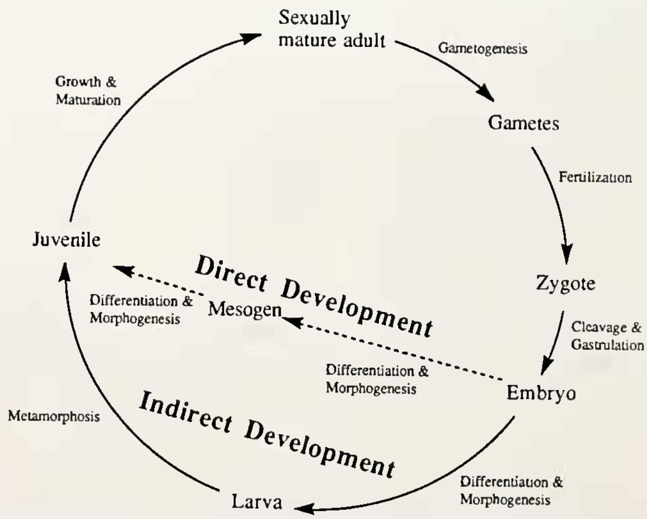

Figure 2. Diagram of an idealized Metazoan life cycle. Small typeface identifies the major life cycle processes (*e.g.*, Differentiation & Morphogenesis); medium-sized typeface identifies the major life cycle stages (*e.g.*, Juvenile); large typeface indicates the two alternative types of development in the life cycle (*e.g.*, Direct Development). See the text sections Life Cycle Terminology, Direct and Indirect Development in Asteroids, and What is a Larva, and What is Not? for definitions and explanations of life cycle features in asteroids.

indirect development. Direct modes of development can involve short, simple ontogenetic sequences or long, complex ones. All that is required for direct development is that larval stages be absent from the life cycle. If larval stages are absent, then metamorphosis does not occur because there is not a definitive morphological stage to be transformed into the juvenile. Thus, direct development, as defined here, is equivalent to "ametamorphic" development (Bonar, 1978). In contrast to indirect development, the juvenile develops progressively (directly) from the embryo, through a series of intermediate stages, all of which are transitional towards the juvenile and without morphogenesis of any larval structures. Since there is not a generally accepted term to apply to these intermediate ontogenetic stages and the term "larva" only refers to a specialized stage in the indirect pattern of development, it seems useful to introduce the term "mesogen" (≈middle stage) to refer to the developmental stages that occur between the embryo and the juvenile in the direct pattern of development. This recognizes that even with direct development there can be a prolonged period of development before the definitive juvenile stage is reached. This term is especially useful where stages of direct development are free-living (*e.g., Pteraster tesselatus,* McEdward, 1992).

Direct and Indirect Development in Asteroids

The distinction between direct and indirect development has been widely used to characterize asteroid developmental patterns. This is potentially useful for the study of evolutionary changes in development because it involves only morphological criteria, rather than ecological ones. However, inconsistent application of these terms (Table III) has led to considerable confusion.

Originally, development via a larval stage was termed indirect and development without a larval stage was described as direct. Habitat and nutrition were not considered relevant to the distinction. Masterman described the brooded development of *Henricia sanguinolenta* as ". . . enabling development to proceed independently of the capture or acquirement of food. But although this is the case, there is to be discerned no essential difference in the course of development which would justify the application of a term like 'direct' development, . . . The presence of lecithal nutrition, like that of haemal nutrition in viviparous forms, no doubt accounts for certain marked adaptations not unlike those characteristics of parasites, such as loss of alimentation, sensory and motor organs, but there can be little question that the larval 'entity' is evident both in space and time in these demersal forms equally with the pelagic" (Masterman, 1902, p.384). *Henricia sanguinolenta* has a brachiolarian stage that remains within a brood protected by the parent during development. However, because it possesses purely larval structures (brachiolar arms, bilateral symmetry), development is indirect.

Table III

Varying application of the terms direct and indirect development in asteroids

Reference	Indirect	Direct
Chia (1968)	Feeding, pelagic development	Nonfeeding development
Mileikovsky (1974)	Pelagic or demersal development	Benthic development
Komatsu (1975)	Bipinnaria + brachiolaria	Brachiolaria only
Oguro *et al.* (1988)	Bipinnaria + brachiolaria[1]	Brachiolaria only[1]
McEdward and Janies	Possesses larval structures	Lacks larval structures

[1] The paxillosids, which have a bipinnaria only or a barrel-shaped larva, were considered as having neither direct nor indirect development, but were placed in a third category, nonbrachiolarian development.

Vestigial larval structures or larval bilateral symmetry are sufficient to characterize asteroid development as indirect. Fell (1945, p.88) stated that "We have now reached the critical point in development at which the forms with direct development diverge from the forms with a larval stage or with a vestige of a larva. Whereas the former proceed to adopt radial symmetry immediately after the conclusion of gastrulation, the latter begin to assume bilateral symmetry, and retain it for a greater or lesser period till it is finally obliterated by radial symmetry." Fell's interest was in the evolution of echinoderm development (especially ophiuroids) and he used an exclusively morphological criterion for direct development.

A significant change occurred when Chia (1968, p.363; see also pp: 359–361) introduced an ecological criterion for indirect development: "Larval nutrition was used as a major criteria to define the types of development. Animals undergoing indirect development are those who have planktotrophic larva resulting from small and less yolky eggs, while animals undergoing direct development are those who have lecithotrophic larva resulting from large and yolky eggs." This change probably reflected two things: (1) an attempt to distinguish between the complex larval morphology characteristic of feeding development and the simpler larval morphology of nonfeeding development; and (2) an attempt to distinguish major patterns of development on the basis of important ecological differences. Whatever the intention, the effect was to introduce considerable confusion into the dichotomy between direct and indirect development. Mileikovsky (1971, 1974, p.172, 175) proposed an ecologically based scheme for classification of developmental patterns in marine invertebrates. He listed four major patterns: pelagic development, demersal development, direct development, and viviparity, and defined direct development solely on the basis of habitat: "Direct development. Larva develops within the egg-spawn until hatching into a fully formed juvenile bottom form. Therefore, larval development of the species is completely under the protection of the egg-envelopes and the spawn-substances. (Pelagic larval phase is omitted)." Mileikovsky (1974, p.172). In these examples, different and inconsistent sets of criteria were used to define these patterns, thus effectively removing any meaningful morphological interpretation of direct development.

Indirect development is usually restricted to cases of feeding larval development (*e.g.*, Wray and Raff, 1991, p.45). This is particularly true for asteroids (Komatsu, 1975; Oguro *et al.*, 1976, 1988). "Development having brachiolaria only, irrespective of whether it is pelagic or benthic, is called the direct type. Development which passes through both the bipinnaria and the brachiolaria is called the indirect type." (Oguro *et al.*, 1976, p.571).

Differing criteria for direct and indirect development create a problem because these patterns of development are intimately tied to the definition of a larva. Does this mean that nonfeeding or benthic larvae are not really larvae after all? Chia argued that ". . . it is indirect development when there is a larval stage and it is direct development when a larval stage is lacking. This definition seems clear and simple but in practice there has been much confusion. The main problem, as I see it, lies in differences of defining what is a larva and much confusion would be reduced if the term 'larva' is clarified" (Chia, 1974, p.121).

What is a Larva, and What is Not?

Chia (1974) proposed a definition for the term "larva." "Larva is a developmental stage, occupying the period from post embryonic stage to metamorphosis, and it differs from the adult in morphology, nutrition, or habitat. In this definition, post embryonic designates the time after emerging (hatching) from the primary egg membrane; prior to that it is considered as embryonic stage" (Chia, 1974, p.122). Chia explicitly rejected the idea that a larva had to possess purely "larval" structures. This was necessary to encompass the ecological sense of a larva as a dispersive propagule. In this regard, Chia was following Vannucci (1959), who had reviewed the various definitions of the term larva that had been used previously and had rejected the common definition of a larva as a developmental stage that had transitory or larval organs. Vannucci's intention was "to use the word larva in a very broad sense, and will thus include many organisms that would not be considered a larva by authors giving to this word a restricted meaning" (Vannucci, 1959, p.7). He cited as examples of organisms that had larvae only by the ecological criterion, the planula, actinula, and ephyrae of cnidarians. Vannucci (1959) defined larva as "a developmental stage, as a rule sexually immature, which may or may not be endowed with special larval organs and which always differs sensibly from the adult" (p.9). The rationale for this broad definition of the term larva was a practical one: the preparation of a comprehensive catalogue of marine larvae (*i.e.*, pelagic dispersive propagules). At the time that it was proposed, the broad, ecological definition of a larva was recognized as "a point of dispute" (Vannucci, 1959, p.7). Chia (1974) improved on Vannucci's definition by making the language less ambiguous. He maintained the ecological sense of a larva by making morphology, nutrition, and habitat alternative criteria by which to define a larva. The advantage of this broader definition is that it recognizes the important ecological roles played by many "larvae" (*i.e.*, feeding and dispersal). This was consistent with the current emphasis on larval ecology and the adaptive significance of developmental patterns in marine benthic invertebrates.

The disadvantage of such an expanded definition of a larva is that by allowing three alternative characters to define a larva (morphology or nutrition or habitat) the definition becomes ambiguous. Under this broad definition, nutritional type or habitat could suffice to define a larva (indirect development), without regard to the nature of morphological development. In addition, numerous applications of the ecological characterization of a larva have involved logical errors, in that negation of only one of the criteria (morphology *or* nutrition *or* habitat), rather than all of the criteria (morphology *and* nutrition *and* habitat), have been used to designate development as nonlarval (*i.e.*, direct).

The problem is seen clearly with regard to brooded development in which young stages can be larval by morphological and developmental criteria (indirect development) but do not live in the plankton and thus do not provide larval dispersal (*e.g.*, *Leptasterias hexactis*, Chia, 1968; *Asterina pseudoexigua pacifica*, Komatsu *et al.*, 1990; *Henricia* sp., Chia and Walker, 1991). On the other hand, there are pelagic propagules that undergo direct development and thus qualify as larvae only in the sense that they are dispersed by water movements (*e.g.*, *Pteraster tesselatus*, McEdward, 1992).

Of the four ecological patterns of development described above (Table I), which necessarily have or do not have larval stages and which can potentially have larvae? Planktotrophic development must include a larval stage in order to possess the structures necessary for food particle capture. In the other four patterns, indirect or direct development are evolutionary options. Pelagic lecithotrophy generally involves larval stages with specialized swimming or settlement structures, but direct development could occur in the plankton via a pelagic mesogen. Demersal development could involve feeding or nonfeeding larvae, as well as direct-developing mesogens. Benthic brooding often involves well-developed larval stages, some brooded young have simplified larval features, but brooding rarely proceeds by strictly direct development. In numerous cases, brooding involves stages with larval structures (sometimes reduced but often functional). This makes the classification of developmental stages as larvae or mesogens difficult; however it is important to realize that there cannot be an absolute distinction between larvae and mesogens, because the evolution from indirect to direct development usually involves the successive reduction and elimination of larval structures. The closest approximation to truly direct development in the asteroids is in the highly derived pterasterids which lack all larval structures, as well as bilateral symmetry, and are thus fundamentally different from all other starfish (McEdward, 1992; McEdward, in prep.; Janies and McEdward, in review).

To answer the question raised in the heading to this section, only a larva (in the strictest morphological and developmental sense) is a larva, and everything else—including a mesogen—is not.

Classification of Developmental Patterns of Asteroids

We propose a multifactor classification scheme for asteroid developmental patterns (Table IV). There are three completely independent characters by which developmental patterns are classified. First, the morphological nature of development can be described using the distinction between indirect and direct development, in the strict sense outlined above. In our scheme, all indirect types have larvae and all direct types do not, regardless of habitat or mode of nutrition during development. Second, developmental patterns can be distinguished by habitat, using the pelagic or benthic distinction. Third, the distinction between feeding and nonfeeding development provides information about nutrition. All three characters must be used to unambiguously describe or classify a developmental pattern.

Eight different developmental patterns can potentially be described when three characters exist, each with two alternative states. Of these eight potential patterns, only six are known to occur in asteroids (Table IV). Indirect development via pelagic feeding larvae is common in asteroids, and it can involve either bipinnarian and brachiolarian stages (*e.g., Asterias rubens,* Gemmill, 1914) or only bipinnarian stages (*e.g., Astropecten scoparius,* Oguro *et al.,* 1976). Indirect development via pelagic nonfeeding larvae can involve a simplified brachiolaria or the barrel-shaped larva. Indirect development on the benthos with a feeding larva possibly occurs in the Antarctic asteroid *Odontaster validus,* but this is uncertain (Pearse and Bosch, 1986). Indirect development via a benthic nonfeeding larva is common among brooding asteroids (*e.g., Ctenodiscus australis,* Lieberkind, 1926; *Henricia sanguinolenta,* Masterman, 1902; *Leptasterias hexactis,* Chia, 1968). Strict direct development is extremely rare in asteroids. Pelagic nonfeeding direct development occurs only in *Pteraster tesselatus* (McEdward, 1992). Benthic nonfeeding direct development has not been reported, but we infer it for the brooding pterasterid, *Pteraster militaris* (Kaufman, 1968; McClary and Mladenov, 1990), based on similarities with *P. tesselatus* (McEdward, in prep.). Construction of the proposed multifactor classification scheme was stimulated, in large part, by the need to clarify the developmental differences between pterasterids and other asteroids with nonfeeding patterns of development. Direct development involving feeding has not been reported for asteroids. Given the predatory nature of most juvenile and adult asteroids, it is unlikely that transitional developmental stages (meso-

Table IV

Multifactor classification of asteroid development patterns

Developmental pattern: Characters — Type	Habitat	Nutrition	Developmental stage and morphology	Asteroid examples[1]
Indirect	Pelagic	Feeding	Complex bipinnarian + brachiolarian larva	*Asterias rubens*
			Complex bipinnarian larva	*Astropecten scoparius*
Indirect	Pelagic	Nonfeeding	Simple brachiolarian larva	*Solaster endeca*
			Simple barrel-shaped larva	*Astropecten gisselbrechti*
Indirect	Benthic	Feeding	Complex bipinnarian + brachiolarian larva	*Odontaster validus?*
Indirect	Benthic	Nonfeeding	Simple brachiolarian larva	*Lepasterias hexactis*
				Asterina minor
Direct	Pelagic	Feeding	—	none known
Direct	Pelagic	Nonfeeding	Simple nonbrachiolarian mesogen	*Pteraster tesselatus*
Direct	Benthic	Feeding	—	none known
Direct	Benthic	Nonfeeding	Simple nonbrachiolarian mesogen	*Pteraster militaris*

[1] The examples provide a cross reference to those cited in the body of the paper. These examples are not exhaustive but were chosen because the references provide good documentation of the various characters used.

gens) could acquire particulate food without the use of specialized (*i.e.*, larval) feeding structures. Direct development, with feeding seems to be an unlikely evolutionary option for starfish.

Evolution of Developmental Patterns in Asteroids

Although indirect development with a complex, feeding, pelagic larva is considered the ancestral condition for echinoderms (Jägersten, 1972; Strathmann, 1978), there has been considerable debate over the nature of the ancestral asteroid life cycle (Bather 1921a, b, 1923; MacBride, 1921, 1923a, b; Mortensen, 1922, 1923). Until recently, it was widely accepted that indirect development via a pelagic feeding bipinnaria with complex larval morphology, but without a brachiolaria stage, characterized the original developmental pattern of asteroids (Fell, 1967, p.S71; Oguro *et al.*, 1988). This argument was first developed by Mortensen (1921, p.219–220), and it was largely based on the absence of the brachiolarian stage in the paxillosids (esp. Luidiidae and Astropectinidae). Paxillosids were considered to be the most primitive of the starfish orders, so the lack of a brachiolarian larval stage was interpreted as the original condition for the asteroids (Oguro *et al.*, 1988). The brachiolaria was thought to have evolved later, at about the same time as the appearance of suckered podia (Fell, 1967, p.S71). The importance of the taxonomic position of the paxillosids in this argument was clearly pointed out by Mortensen (1923, p.323): "I have no direct interest in maintaining the Brachiolaria to be a secondarily specialized larval type. If conclusive proof is given that the Brachiolaria is the primitive, the Astropectinid-larva the specialized form, I shall not hesitate to drop my present view. But I must maintain that this view is not unjustified by the facts so far known." In contrast, MacBride (1921, 1923b) argued that paxillosids were specialized, not primitive, and he explained the lack of a brachiolarian larva as an adaptation for life on soft substrata. This view was strengthened by the discovery that some paxillosids have suckered podia for a short period immediately after metamorphosis (*Astropecten latespinosus*, Komatsu, 1975, p.53; *Astropecten scoparius*, Oguro *et al.*, 1976, p.567). The recent analyses of paxillosid biology by Blake (1987, 1988) have provided convincing support to the view that paxillosids are highly derived asteroids with body form, digestive, podial, as well as developmental, specializations for life in sandy and muddy habitats. We accept this view and consider the original asteroid life cycle to have consisted of pelagic feeding indirect development via a complex bipinnaria and a complex brachiolaria (Fig. 1A, B, 3, 4).

All of the other developmental patterns that occur in asteroids (Table IV) can be derived by means of six different evolutionary transitions (Fig. 3). Loss of larval feeding (transition A) eliminated the bipinnaria from the life cycle and resulted in a pelagic, nonfeeding brachiolaria. Associated with the loss of larval feeding structures, such as ciliated bands, bipinnarian arms, and a functional gut, the morphology of the brachiolaria was greatly simplified (Fig. 1C). However, the larva retained bilateral symmetry, brachiolar arms, and many features of internal development (*e.g.*, coelom formation) characteristic of the more complex bipinnarian and brachiolarian forms. This has occurred at least 6–9 times in the asteroids (Strathmann, 1978). Indirect development via a simple brachiolarian larva is known to occur in four orders: Forcipulatida, Valvatida, Spinulosida, and Velatida (Fig. 4). From this pelagic, nonfeeding pattern of development, a second evolutionary change (transition B, Fig. 3) eliminated the pelagic phase of development and resulted in benthic development via brooding, or a free-living demersal larva. This resulted in an indirect pattern of development with a nonfeeding brachiolarian larva and is known from the orders Forcipulatida, Valvatida, Spinulosida, and Velatida (Fig. 4).

Direct development, in the strict sense that we use the term, is known among asteroids only in the family Pterasteridae. We postulate that direct development evolved in a lineage of brooders within the order Velatida (Fig. 4). Brooding is rare in solasterids, but is presumed to be the predominant mode of development in the other velatid families: Korethrasteridae, Caymanostellidae, Myxasteridae, and Pterasteridae. Unfortunately, because these are mostly deep-sea organisms, very little is known about their development (Clark and Downey, 1992). Larval attachment structures were likely lost in the pterasterids as the lineage became specialized in the deep-sea and evolved brooded young. Direct development was probably the result of selection for general developmental efficiency (*i.e.*, the discontinuance of vestigial larval programs) during a long history of brooding. Extreme simplification of development (transition C, Fig. 3), eliminated all of the larval features (*e.g.*, brachiolar arms, bilateral symmetry) from the life cycle and produced an ontogenetic sequence leading directly from the embryo to the juvenile (Fig. 2). Intermediate developmental stages represent mesogens (Fig. 1F) that are brooded by the parent. The developmental pattern is benthic, nonfeeding, and direct (Table IV) and it is known for only a single species, *Pteraster militaris* (Kaufman, 1968; McEdward, in prep.) (Fig. 4). A subsequent modification of this pattern of direct development involved the re-evolution of a pelagic period during development (transition D, Fig. 3). This produced the unique type of pelagic, nonfeeding "larva" of *Pteraster tesselatus* (McEdward, 1992). This pelagic developmental stage is a mesogen (*not* a larva) and the pattern of development is direct, pelagic, and nonfeeding (Table IV). The pelagic mesogen of *Pteraster tesselatus* is fundamentally different from the pelagic, nonfeeding brachiolarian larva of other starfish. Important differences include: absence of bra-

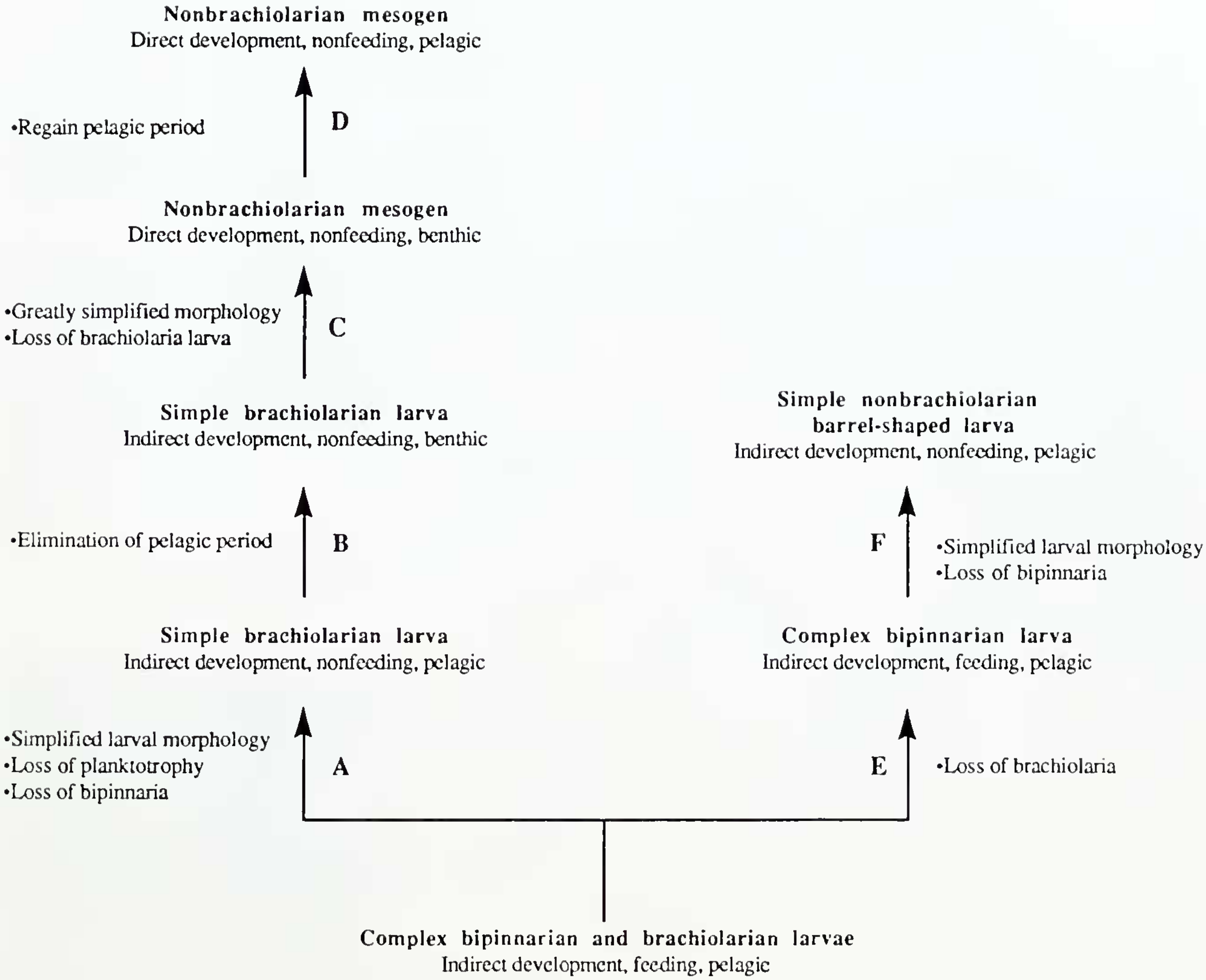

Figure 3. Postulated sequences of evolutionary transitions in asteroid life cycles that account for the diversity of larval types and developmental patterns. Bold typeface identifies the larval types (*e.g.*, Complex bipinnarian larva); associated plain typeface indicates the developmental pattern (*e.g.*, Indirect development, feeding, pelagic; see Table IV); bulleted lists and bold typeface uppercase letters identify the changes in development associated with each evolutionary transition (*e.g.*, E; •Loss of brachiolaria).

chiolar arms and attachment disk, use of podia for attachment at settlement, a novel pattern of coelom formation and water-vascular morphogenesis, radial rather than bilateral symmetry, parallel embryonic, mesogen, and adult axes of symmetry, and a transverse orientation of the juvenile disk (Janies and McEdward, in review; McEdward, 1992). Note that our interpretation of the development of *P. tesselatus* is radically different from the currently accepted view. Chia (1966, pp.507–508) originally described this species as developing via a nonfeeding bipinnaria. Others have interpreted the pelagic stage as a modified lecithotrophic brachiolaria (Fell, 1967, p.S71; Oguro *et al.*, 1988, p.242). Detailed evidence supporting our interpretation will be presented elsewhere (McEdward, in prep.; Janies and McEdward, in review).

An entirely unrelated sequence of evolutionary changes has occurred in the paxillosids. All paxillosids lack the brachiolaria (Fig. 4). The pattern of development involving only a complex feeding bipinnarian larva (Table IV) evolved from the ancestral asteroid life cycle by loss of the brachiolarian stage (transition E, Fig. 3). This interpretation is different from that of Oguro *et al.* (1988, p.243) who claim that "the bipinnaria is the original or primitive type of sea-star larva." This view that the ancestral asteroid life cycle lacked the brachiolaria stage is inconsistent with the recent analysis of the paxillosids as a highly derived group of asteroids (see above). Loss of the brachiolaria was undoubtedly associated with specialization for life on soft substrata by the paxillosids; adhesive structures would not provide anchorage for settle-

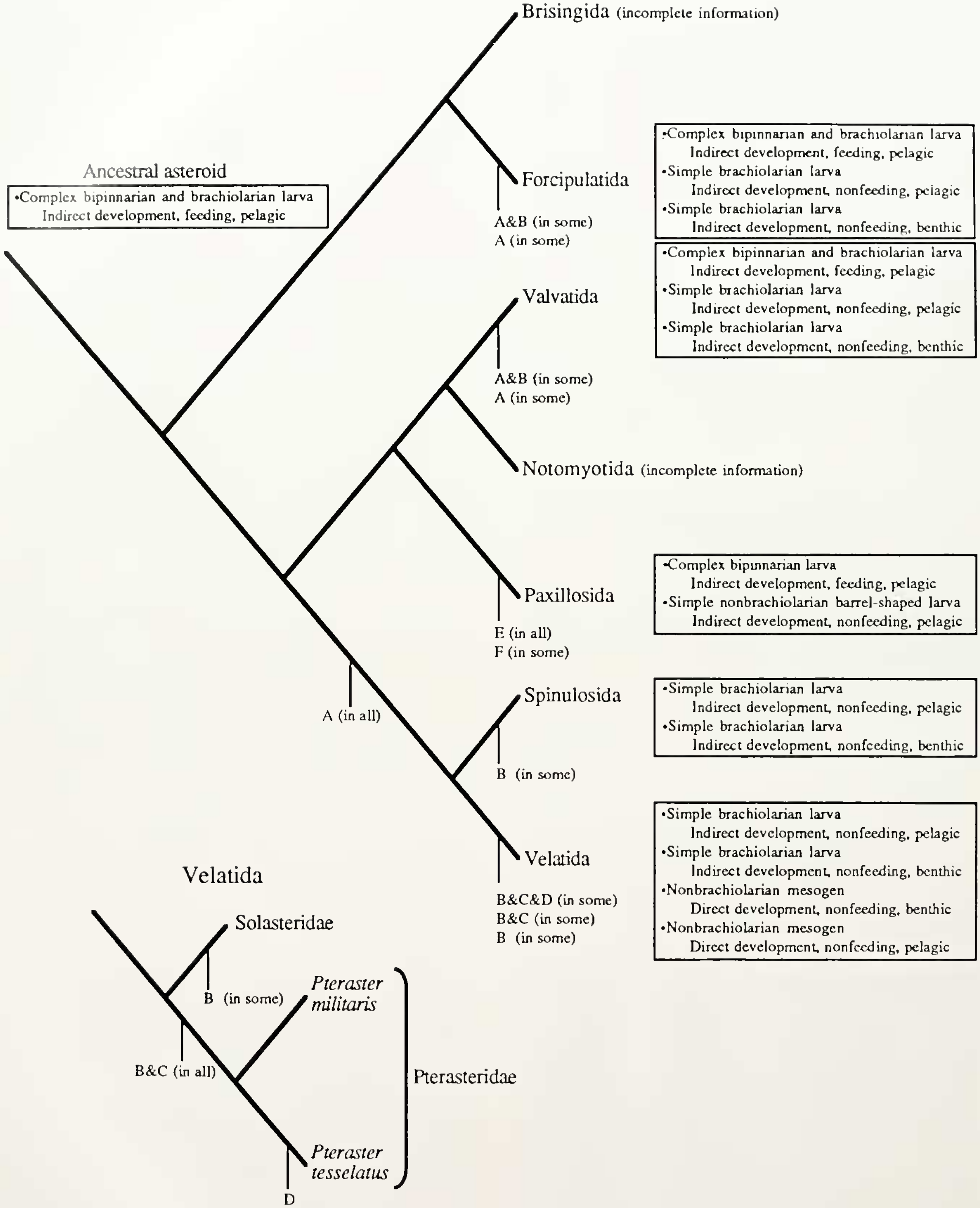

Figure 4. Phylogenetic distribution of larval types and developmental patterns among asteroid orders (large cladogram) and within selected groups of velatids (small cladogram). Phylogenetic relationships are based on Blake (1987). Boxed text lists the different larval types and developmental patterns for each clade (*e.g.*, •Complex bipinnarian and brachiolarian larva; Indirect development, feeding, pelagic; see Table IV). See text for examples and references. Uppercase letters on the branches of the cladograms indicate probable occurrences of evolutionary transitions that can account for the distribution of larval types and developmental patterns (*e.g.*, A & B; see Fig. 3).

ment on mud or sand. Evolutionary loss of larval feeding and the resulting morphological simplification (transition F, Fig. 3) produced the barrel-shaped larva (Fig. 1G). This is the only type of nonfeeding development known in the paxillosids (Fig. 4). The barrel-shaped larva is clearly modified from the bipinnaria (Komatsu *et al.*, 1988).

Summary

Explicit definitions of life cycle terminology and our multifactor classification scheme for developmental patterns help focus attention on the morphological features of development. We believe that this provides a clearer conceptual basis for the analysis of asteroid life cycle evolution. Our hypothesis for the evolutionary transitions in development can account for the diversity of larval forms and developmental patterns in starfish. More importantly, we hope that they stimulate further exploration, analysis, and discussion of the evolution of asteroid development.

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Literature Cited

Agassiz, A. 1877. Embryology of the starfish. *Mem. Mus. Comp. Zool.* **5:** 1–83.

Atwood, D. G. 1973. Larval development of the asteroid, *Echinaster echinophorus. Biol. Bull.* **144:** 1–11.

Barker, M. F. 1978. Structure of the organs of attachment of brachiolaria larvae of *Stichaster australis* (Verril) and *Coscinasterias calamaria* (Gray) (Echinodermata: Asteriodea). *J. Exp. Mar. Biol. Ecol.* **33:** 1–36.

Bather, F. A. 1921a. Echinoderm larvae and their bearing on classification. *Nature* **108:** 459–460.

Bather, F. A. 1921b. Echinoderm larvae and their bearing on classification. *Nature* **108:** 530.

Bather, F. A. 1923. Echinoderm larvae and their bearing on classification. *Nature* **111:** 397.

Birkeland, C., F.-S. Chia, and R. R. Strathmann. 1971. Development, substratum selection, delay of metamorphosis and growth in the seastar, *Mediaster aequalis* Stimpson. *Biol. Bull.* **141:** 99–108.

Blake, D. B. 1987. A classification and phylogeny of post-Palaeozoic sea stars (Asteroidea: Echinodermata. *J. Nat. Hist.* **21:** 481–528.

Blake, D. B. 1988. Paxillosidans are not primitive asteroids: a hypothesis based on functional considerations. Pp. 309–314 in *Echinoderm Biology*, R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, eds. A. A. Balkema, Rotterdam.

Bonar, D. B. 1978. Morphogenesis at metamorphosis in opisthobranch molluscs. Pp. 177–196 in *Settlement and Metamorphosis of Marine Invertebrate Larvae*, F.-S. Chia and M. E. Rice eds. Elsevier-North Holland, Amsterdam.

Bonner, J. T. 1988. *The Evolution of Complexity.* Princeton University Press, Princeton.

Bosch, I. 1989. Contrasting modes of reproduction in two Antarctic asteroids of the genus *Porania*, with a description of unusual feeding and non-feeding larval types. *Biol. Bull.* **177:** 77–82.

Buss, L. W. 1987. *The Evolution of Individuality.* Princeton University Press, Princeton.

Byrne, M. 1991. Developmental diversity in the starfish genus *Patirella* (Asteroidea: Asterinidae). Pp. 499–508 in *Biology of Echinodermata*, T. Yanagisawa, I. Yasumasu, C. Oguro, N. Suzuki, and T. Motokawa eds. A. A. Balkema, Rotterdam.

Byrne, M., and M. F. Barker. 1991. Embryogenesis and larval development of the asteroid *Patiriella regularis* viewed by light and scanning electron microscopy. *Biol. Bull.* **180:** 332–345.

Chia, F.-S. 1966. Development of a deep-sea cusion star, *Pteraster tesselatus. Proc. Cal. Acad. Sci.* **34:** 505–510.

Chia, F.-S. 1968. The embyrology of a brooding starfish, *Leptasterias hexactis* (Stimpson). *Acta Zool.* **49:** 321–364.

Chia, F.-S. 1969. Reproductive biology of an intraovarian brooding starfish, *Patiriella vivipera* Dartnall. *Am. Zool.* **16:** 181.

Chia, F.-S. 1974. Classification and adaptive significance of developmental patterns in marine invertebrates. *Thalassia Jugoslav.* **10:** 121–130.

Chia, F.-S., and C. W. Walker. 1991. Echinodermata: Asteroidea. Pp. 301–353 in *Reproduction of Marine Invertebrates*, Vol. VI, *Echinoderms and Lophophorates*, A. C. Giese, J. S. Pearse, and V. B. Pearse eds. Boxwood Press, Pacific Grove, CA.

Clark, A. M., and M. E. Downey. 1992. *Starfishes of the Atlantic.* Chapman and Hall, New York.

Emlet, R. B., L. R. McEdward, and R. R. Strathmann. 1987. Echinoderm larval ecology viewed from the egg. Pp. 55–136 in *Echinoderm Studies*, M. Jangoux, and J. M. Lawrence, eds. A. A. Balkema, Rotterdam.

Fell, H. B. 1945. A revision of the current theory of echinoderm embryology. *Trans. R. Soc. N. Z.* **75:** 73–101.

Fell, H. B. 1967. Echinoderm ontogeny. Pp. 60–85 in *Treatise on Invertebrate Paleontology, Part S, Echinodermata*, R. C. Moore, ed. GSA and University of Kansas Press, Lawrence.

Fisher, W. K. 1911. Asteroidea of the North Pacific and adjacent waters. *U. S. Natl. Mus. Bull.* **76:** 1–405.

Gemmill, J. F. 1912. The development of the starfish *Solaster endeca* Forbes. *Trans. Zool. Soc. Lond.* **20:** 1–71.

Gemmill, J. F. 1914. The development and certain points in the adult structure of the starfish *Asterias rubens.* L. *Phil. Trans. R. Soc. Lond.* **205B:** 213–294.

Gemmill, J. F. 1915. The larva of the starfish *Porania pulvillus* (O.F.M.). *Q. J. Microsc. Sci.* **61:** 27–50.

Gemmill, J. F. 1920. The development of the starfish *Crossaster papposus*, Müller and Troschel. *Q. J. Microsc. Sci.* **64:** 155–190.

Grahme, J., and G. M. Branch. 1985. Reproductive patterns of marine invertebrates. *Oceanog. Mar. Biol. Ann. Rev.* **23:** 373–398.

Hörstadius, S. 1939. Uber die Entwicklung von *Astropecten aranciacus.* L. *Pubbl. Staz. Zool. Napoli.* **17:** 221–312.

Hyman, L. H. 1955. *The Invertebrates.* Vol. IV. *Echinodermata.* McGraw-Hill, NY.

Jablonski, D., and R. A. Lutz. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol. Rev.* **58:** 21–89.

Jägersten, G. 1972. *The Evolution of the Metazoan Life Cycle, A Comprehensive Theory.* Academic Press, London and New York.

Kaufman, Z. S. 1968. The postembryonic period of development of some White Sea starfish. *Dolkady Biol. Sci.* **181:** 507–510.

Komatsu, M. 1975. On the development of the sea-star, *Astropecten latespinosus* Meissner. *Biol. Bull.* **148:** 49–59.

Komatsu, M. 1982. Development of the sea-star *Ctenopleura fisheri. Mar. Biol.* **66:** 199–205.

Komatsu, M., and S. Nojima. 1985. Development of the seastar, *Astropecten gisselbrechti* Doderlein. *Pac. Sci.* **39:** 274–282.

Komatsu, M., M. Murase, and C. Oguro. 1988. Morphology of the barrel-shaped larva of the sea-star, *Astropecten latespinosus.* Pp. 267–272 in *Echinoderm Biology,* R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, eds. A. A. Balkema, Rotterdam.

Komatsu, M., Y. T. Kano, H. Yoshizawa, S. Akabane, and C. Oguro. 1979. Reproduction and development of the hermaphroditic seastar, *Asterina minor* Hayashi. *Biol. Bull.* **157:** 258–274.

Komatsu, M., Y. T. Kano, and C. Oguro. 1990. Development of a true ovoviviparous sea star, *Asterina pseudoexigua pacifica* Hayashi. *Biol. Bull.* **179:** 254–263.

Kume, M., and K. Dan. 1968. *Invertebrate Embrology.* National Technical Information Services, Springfield, VA.

Lieberkind, I. 1926. *Ctenodiscus australis* Lütken. A brood-protection asteroid. *Vid Medd Dansk. Hist. Foren.* **82:** 184–196.

Ludwig, H. 1882. Entwicklungsgeschichte der Asterina gibbosa Forbes. *Zeitschrift Zool.* **37:** 1–98.

MacBride, E. W. 1896. The development of *Asterina gibbosa. Q. J. Microsc. Sci.* **38:** 339–411.

MacBride, E. W. 1914. *Textbook of Embryology, Vol. I, Invertebrata.* MacMillan and Co. London.

MacBride, E. W. 1921. Echinoderm larvae and their bearing on classification. *Nature* **108:** 529–530.

MacBride, E. W. 1923a. Echinoderm larvae and their bearing on classification. *Nature* **111:** 47.

MacBride, E. W. 1923b. Echinoderm larvae and their bearing on classification. *Nature* **111:** 323–324.

Margulis, L. 1990. Kingdom Animalia: the zoological malaise from a microbial perspective. *Am. Zool.* **30:** 861–875.

Masterman, A. T. 1902. The early development of *Cribrella oculata* (Forbes) with remarks on echinoderm development. *Trans. R. Soc. Edin.* **40:** 373–418.

McClary, D. J., and P. V. Mladenov. 1990. Brooding biololgy of the sea star *Pteraster militaris* (O. F. Müller): energetic and histological evidence for nutrient translocation to brooded juveniles. *J. Exp. Mar. Biol. Ecol.* **142:** 183–199.

McEdward, L. R. 1992. Morphology and development of a unique type of pelagic larva in the starfish *Pteraster tesselatus* (Echinodermata: Asteroidea). *Biol. Bull.* **182:** 177–187.

Mileikovsky, S. A. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar. Biol.* **10:** 193–213.

Mileikovsky, S. A. 1974. Types of larval development in marine bottom invertebrates: an integrated ecological scheme. *Thalassia Jugoslav.* **10:** 171–179.

Mortensen, T. 1898. Die echinodermenlarven der plankton-expedition. *Ergebnisse der Plankton-Expedition der Humbolt-Stiftung.* Bd. II. J. Verlag von Lipsius and Tischer, Kiel and Leipzig.

Mortensen, T. 1921. *Studies on the Development and Larval Forms of Echinoderms.* G. E. C. Gad, Copenhagen.

Mortensen, T. 1922. Echinoderm larvae and their bearing on classification. *Nature* **110:** 806–807.

Mortensen, T. 1923. Echinoderm larvae and their bearing on classification. *Nature* **111:** 322–323.

Oguro, C., M. Komatsu, and Y. Kano. 1976. Development and metamorphosis of the sea star *Astropecten scoparius* Valenciennes. *Biol. Bull.* **151:** 560–573.

Oguro, C., M. Komatsu, and Y. Kano. 1988. Significance of the nonbrachiolarian type of development in sea stars. Pp. 241–246 in *Echinoderm Biology,* R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, eds. A. A. Balkema, Rotterdam.

Osterud, H. L. 1918. Preliminary observations on the development of *Leptasterias hexactis. Publ. Puget Sound Biol. Sta.* **2:** 1–15.

Palmer, A. R., and R. R. Strathmann. 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia* **48:** 308–318.

Pearse, J. S., and I. Bosch. 1986. Are the feeding larvae of the commonest antarctic asteroid really demersal? *Bull. Mar. Sci.* **39:** 477–484.

Strathmann, M. F. 1987. *Reproduction and Development of the Marine Invertebrates of the Northern Pacific Coast.* University of Washington Press, Seattle.

Strathmann, R. R. 1974. Introduction to function and adaptation in Echinoderm larvae. *Thalassia Jugoslav* **10:** 321–339.

Strathmann, R. R. 1978. The evolution and loss of feeding larval stages of marine invertebrates. *Evolution* **32:** 894–906.

Strathmann, R. R., and M. F. Strathmann. 1982. The relationship between adult size and brooding in marine invertebrates. *Am. Nat.* **119:** 91–101.

Strathmann, M. F., R. R. Strathmann, and D. J. Eernisse. 1988. A new species of *Henricia,* Gray 1840, in the Northeastern Pacific. P. 813 in *Echinoderm Biology,* R. D. Burke, P. V. Mladenov, P. Lambert, and R. L. Parsley, eds. A. A. Balkema, Rotterdam.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.* **25:** 1–45.

Vannucci, M. 1959. Catalogue of marine larvae. Universidade de Sao Paulo. Instituto Oceanografico. 7-11.

Wilson, D. P. 1978. Some observations on bipinnariae and juveniles of the starfish genus *Luidia J. Mar. Biol. Assoc.* (U.K.). **58:** 467–478.

Wray, G. A., and R. A. Raff. 1991. The evolution of developmental strategy in marine invertebrates. *T. R. E. E.* **6:** 45–50.

Yamaguchi, M., and J. S. Lucas. 1984. Natural parthenogenesis, larval and juvenile development, and geographical distribution of the coral reef asteroid *Ophidiaster granifer. Mar. Biol.* **83:** 33–42.